Title

Multiple evolutionary routes to monogamy: modelling the co-evolution of mating decisions and parental investment

Key words

mating system; parenting; sexual conflict; polygyny threshold; adaptive dynamics; demography;

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Abstract

The relationships between mating decisions and parental investment are central to evolution, but to date few theoretical treatments of their co-evolution have been developed. Here we adopt a demographically explicit, adaptive dynamics approach to analyse the co-evolution of female mating decisions and parental investment of both sexes in a self-consistent way. Our models predict that where females cannot interfere with one another's mating decisions, and where they do not differ in their survival- and fecundity prospects, monogamy should be rare, and favoured only under harsh environmental conditions, in sparse populations. However, allowing for interference or asymmetries among females leads to selection for monogamy over a much broader range of environments and demographies. Interference by paired, resident females may prevent unmated rivals from joining existing monogamous pairs, thus barring the formation of polygynous groups. Asymmetries between established, primary females and subsequently joining secondary females may increase the relative costs of early polygynous reproduction compared to delayed monogamy for the latter. The models thus highlight different routes by which monogamy may evolve. We further track how parental investment by the sexes co-evolves with female mating decisions, highlighting how sexual conflict over parental investment is both cause and effect of mating behaviour.

Introduction

The range of animal mating systems, from extreme polygamy to life-time monogamy, has intrigued evolutionary biologists for over a century (Shuster and Wade 2003). The broad body of work that has emerged as a result of these research efforts suggests that mating system evolution is intertwined with a wide array of ecological traits (Shuster and Wade 2003). Among others, feedbacks have been suggested between mating and (i) brain size (Dunbar and Shultz 2007), (ii) demography (Lukas and Clutton-Brock 2013), (iii) sociality (Boomsma 2013), and (iv) life-history (Bonduriansky et al. 2008).

The one trait that is identified as important to mating system evolution in all studies is parental investment (Trivers 1972). The reason is that the main cost of increased parental investment, e.g. in the form of extended parental care, is a lowered rate of reproduction, while, conversely, the pursuit of a higher mating rate may result in insufficient parental investment and the failure of reproductive attempts (Shuster and Wade 2003), (Alonzo 2010). Consequently, individuals are expected to try to maximise their own mating rate at the expense of their mates, either by shifting the load of parental investment towards their partners or by increasing the number of partners they mate with (Chapman et al. 2003), (Parker 2006), (Harrison et al. 2009). This issue lies at the core of the fields of the evolution of (a) mating systems (Shuster and Wade 2003), (b) sexual conflict (Chapman 2006), and (c) parental care (Royle et al. 2012).

Much theoretical work has tried to unravel the causal relationships between sexual selection, mating system evolution, and parental investment (reviewed e.g. in: (Kokko and Jennions 2008), (Kokko et al. 2012), (Houston et al. 2013)). Most modelling approaches, however, do not include simultaneous feedback loops between (a) demography, (b) the mating system, and (c) parental investment strategies (but see (Dillard and Westneat 2016), (Fromhage and Jennions 2016) for notable exceptions). In addition, most models focus on one or two specific aspects of mating and parenting and treat all other parameters as fixed. These focal traits include, but are not limited to, (i) physiological or behavioural sex differences (e.g. anisogamy or sex-differential mobility), (ii) operational or adult sex ratios (OSR and ASR, respectively),

and (iii) conflicts within and among the sexes (e.g. sperm competition or conflicts over care). The narrow focus of many existing models has led several authors to argue for more holistic and inclusive theoretical approaches (e.g. (Székely et al. 2000), (Alonzo 2010), (Dillard and Westneat 2016)). The most explicit of these suggestions comes from (Houston et al. 2013) when they say that 'A full model of parental care should be put in the context of life history and ecology, and ultimately have the OSR, extrapair copulations and paternity, mating preferences, mate choice behaviour and care behaviour emerge in a holistic and consistent manner'. This statement is not specific to models of parental care, but rather applies to theoretical approaches investigating any of the biological aspects they list.

Here we report on our development of one such model. We do not incorporate all the parameters requested by (Houston et al. 2013) (see Methods for a complete list of included parameters), but we present a game-theoretical approach in which both the mating system and parental investment strategies co-evolve in a demographically explicit setting (Figure 1). The work is broadly based on classic approaches to mating system evolution (Orians 1969), (Emlen and Oring 1977), (Maynard Smith 1977), (Shuster and Wade 2003), but extends these models by applying an adaptive dynamics approach and allowing for parental investment to co-evolve with mating decisions (Dieckmann and Law 1996), (Dercole and Rinaldi 2008).

As in classic models of the polygyny threshold, we suppose that an unmated female encounters potential breeding males sequentially (at a rate proportional to their density). Because engaging in polygyny is potentially costly, due to a reduction in the amount of paternal investment obtained, a female that encounters a male who is already mated can decide to continue searching for an unpaired male or to accept polygyny and start breeding. Thus, the mating system, i.e. the proportions of monogamously and polygynously paired males, emerges from female mating decisions, and these are (partly) based on demography and male and female parental investment strategies. In turn, both demography and male

and female investment behaviour are (partly) determined by females' mating decisions, closing the feedback loop.

Methods

Model Names & Aims

Below we explore four different model variants, which we will refer to as Models 1-4: a basic variant (Model 1), and three extensions (Models 2, 3 and 4), each of which considers a different potential evolutionary route to monogamy.

Model 2 allows for interference by established monogamously breeding females ('residents' or 'primary' females) in attempts of floating females (potential 'joiners' or 'secondary' females) to join existing pairs. We reason that, where polygyny is potentially costly to females, monogamously paired females may benefit from resisting being joined by another female, e.g. by aggressing potential joiners or inhibiting their mates' ability to attract another female (Eggert and Sakaluk 1995), (Kempenaers 1995), (Sandell and Smith 1997), (Grønstøl et al. 2003). We model the impact of this interference by assuming that the probability of an unmated female joining a mated pair depends upon a weighted average of the fitness impact of this event on both the resident and the joining female, with the weighting coefficient reflecting the relative power of the two females in question (see below for details).

Models 3 and 4 allow for asymmetries between a male's first, primary (resident) mate, and any subsequent, secondary mate. We reason that initially monogamously paired females and those that join a monogamous pair may differ in their fitness prospects, even though they breed alongside each other in the same polygynous group, due to, e.g., differential access to resources within the territory or differential investment by the male (Simmons et al. 1985), (Burley 1988), (Huk and Winkel 2006). We explore two such possible asymmetries in the fitness prospects of residents and joiners in Models 3 and 4: joiners either suffer from lower fecundity (Model 3) or from increased mortality risk (Model 4).

Overview of Model 1

We assume a sexual population of infinite size in which breeding occurs in territories, while non-breeding individuals aggregate in non-localised, sex-specific floater communities (Figure 1). We further assume that each territory can support only one male and up to two females and that all territories are of the same quality. Also, all individuals of identical sex and status (i.e. of the same type or class, see below) are of the same quality. We model the dynamics of the population, i.e. deaths, births, and status changes, in continuous time.

Newly born individuals become floaters and must wait for a vacancy in a territory before they can reproduce. Once an individual acquires breeding status, it remains on its territory until it dies. However, settling in a territory is not guaranteed, as floaters may die before they encounter a territory vacancy.

Vacancies arise whenever a territorial individual dies. Vacancies for males are immediately taken up by floaters, while floating females encounter territories at a rate proportional to their density. This allows for the occurrence of territories occupied by only a solitary male, by a male and a female, or by a male and two females. There are no territories occupied by a solitary female or wholly unoccupied territories.

Upon encountering a solitary male, female floaters will always occupy the associated vacancy to form a monogamous pair. Female floaters that encounter a territory already occupied by a male and a female, however, will only join the focal monogamous pair to form a polygynous group, if doing so yields higher expected fitness than remaining a floater. This assessment of fitness consequences is assumed to be imperfect (see below).

In total, seven classes of individuals exist in the model (floating males, floating females, solitary males, monogamous males, monogamous females, polygynous males, females in polygynous groups). Breeding females, i.e. females in a territory, constantly produce offspring at a specified rate, but offspring

survival (and thus adult fitness) is determined by the parental investment of both parents. Adult mortality is determined by individual class and parental investment expended. This way, we implement a trade-off between adult survival (which is increased by decreasing parental investment) and reproduction (which is increased by increasing parental investment).

Population dynamics

At demographic equilibrium, the frequencies of breeding territories supporting a solitary male, a monogamous pair, or a polygynous group, respectively, and the densities of female and of male floaters are all stable due to an equilibrium of deaths, births, and status changes. Throughout this paper, we denote densities of floaters as L_m (males) and L_f (females; i.e. subscripted letters indicate sex; both densities are measured as floaters per breeding territory; Figure 1). We further denote the frequency of territories as B_0 for those occupied by a solitary male, B_1 for those occupied by a monogamous pair, and B_2 for those occupied by a polygynous group (i.e. subscripted numbers signify the number of females in a given breeding territory). The sex ratio of offspring produced (see below; denoted as $\hat{\theta}$: proportion of males) and the rate at which females encounter territories (see above; denoted as $\hat{\varepsilon}$) are fixed globally.

We allow for different mortalities for individuals of different sex and status (i.e. there are class-specific mortalities); floating males suffer mortality rate μ_{mL}, while the mortality of solitary, monogamous, and polygynous males is denoted as μ_{mB0}, μ_{mB1}, and μ_{mB2}, respectively. The mortality of female floaters is denoted μ_{fL}, and monogamous females and females in polygynous groups suffer mortality rate μ_{fB1} and μ_{fB2}, respectively. All mortality rates are calculated as functions of a baseline mortality ($\hat{\mu}_{mL}$, $\hat{\mu}_{fL}$, $\hat{\mu}_{mB}$, $\hat{\mu}_{fB}$) and the respective parental investment expended by individuals of that sex and status (see below).

We model reproduction as a function of a global rate of producing offspring ($\hat{\gamma}$) and the parental investment expended by both parents (total parental investment). Hence, γ_{B1} denotes the rate of

production of surviving offspring for a monogamous female, and γ_{B2} denotes the rate of production of surviving offspring for a female in a polygynous group (see below). This allows us to simulate environments of different overall productivity/harshness and their impact on the evolution of mating decisions and parental investment (see below and Supplementary Material for details): larger values of $\hat{\gamma}$ increase the rate at which females produce offspring, representing less harsh (and thus more productive) environments. See Figure 1 for a schematic overview of the changes in the frequency of territory types and the densities of floaters.

Reproductive value calculations

In the model, the reproductive value of an individual of any particular class is proportional to the number of surviving offspring expected to be produced over that individual's life span (note that all surviving offspring join the floater pool at birth, and so are of equal expected value). While only paired individuals, i.e. males and females in monogamous pairs or polygynous groups, actually produce offspring, solitary males as well as floating males and females are expected to reach breeding status with certain probabilities. Consequently, all classes of individuals have non-zero expected value, denoted as W_{mL} (floating males), W_{mB0} (solitary males), W_{mB1} (monogamous males), W_{mB2} (polygynous males), W_{fL} (floating females), W_{fB1} (monogamous females), W_{fB2} (females in polygynous groups), respectively. For each class of individual, we calculate the expected future offspring by summing over all possible events (death, status change, reproduction), weighted according to their probabilities of occurrence. For example, a solitary male is either joined by a floating female, thus changing his status to that of monogamous male (at rate $\hat{\varepsilon} * L_f * B_0 * 1/B_0$, resulting in him obtaining a monogamous male's expected number of future offspring W_{mB1}), or he dies (at rate μ_{mB0}, resulting in him receiving no future offspring); a solitary male's value thus satisfies the equation:

Eq. 1: $W_{mB0} = \frac{\hat{\varepsilon} * L_f * B_0 * \frac{1}{B_0} * W_{mB1} + 0 * \mu_{mB0}}{\hat{\varepsilon} * L_f * B_0 * \frac{1}{B_0} + \mu_{mB0}}$

which simplifies to:

Eq. 2: $W_{mB0} = \frac{\hat{\varepsilon} * L_f * W_{mB1}}{\hat{\varepsilon} * L_f + \mu_{mB0}}$

See Supplement 5 for a complete list of comparable reproductive value equations, which can be jointly solved to obtain expressions for the value of each class of individual as a function of other model parameters.

Evolution of parental investment

In order to model the evolution of parental investment, we use an adaptive dynamics approach with separation of ecological and evolutionary time scales (Dieckmann and Law 1996). Thus, we make two key assumptions: first, parental investment expended by a mutant invading the resident population is only marginally different from that expended by residents. Second, competition among invading mutants and residents, and the ensuing changes in frequency, occur over a much shorter time span (ecological or demographic time scale) than the interval at which new mutations arise and invade the population (evolutionary time scale). Consequently, we model evolution as a step-wise process in which the population is always quasi-monomorphic and at demographic equilibrium (Dieckmann and Law 1996).

In the current manuscript, investment in parenting is the focus of a trade-off between reproduction and survival: mortality rates are accelerating functions of parental investment, while rates of production of surviving offspring are saturating functions of parental investment. For example, mortality of monogamous females is given as:

Eq. 3: $\mu_{fB1} = \hat{\mu}_{fB} + (C_{fB1})^2$

where $\hat{\mu}_{fB}$ is the baseline mortality of breeding females (see above) and C_{fB1} is the investment expended by monogamous females. Conversely, reproduction of surviving offspring by a monogamous female is given as:

Eq. 4: $\gamma_{B1} = \hat{\gamma} * (1 - e^{-(C_{fB1}+C_{mB1})})$

where $\hat{\gamma}$ is the global rate of producing offspring (see above), C_{fB1} is the parental investment by monogamous females, and C_{mB1} is the parental investment by monogamous males. See Supplement 4 for a complete list of mortality and reproduction functions used in the current manuscript.

Given our adaptive dynamic assumptions, the rate of evolutionary change in the level of investment by any given class of individual is proportional to the relevant selection gradient, which we calculate as the partial derivative of mutant fitness (for an individual of that class) with respect to the focal individual's own mutant investment level, assuming the population is at demographic equilibrium; expressions for mutant fitness are given in Supplement 7. Note that as all monogamous breeding pairs and polygynous groups are formed by individuals joining from the floater pool (i.e. there is no philopatry), group members are always unrelated. There is consequently no need to consider the impact on the fitness of a focal mutant of correlated changes in the phenotype of other group members.

Evolution of mating decisions

We assume that the mating system is a result of females' acceptance of polygynous matings. Explicitly, we consider the ratio of monogamously to polygynously mated males as indicative of the mating system, i.e. whether the species should be considered monogamous or polygynous. This ratio is determined in part by demographic effects, because monogamy may still be observed even when being strongly selected

against, simply because densities of floating females or encounter rates are too low. More interestingly, though, the mating system is determined by floating females' willingness to join already established monogamous pairs to form polygynous groups. We model this decision as an adaptive behaviour in the sense that females choose whichever life history, remaining a floater or accepting polygyny, yields higher fitness. While this choice is by definition binary, we model it as a probability between 0 and 1, the actual value of which is calculated as:

Eq. 5: $\hat{J} = \frac{1}{1+e^{-\hat{\beta}*(W_{fB2}-W_{fL})}}$

where $\hat{J}$ is the probability that a floating female joins a monogamous pair, $\hat{\beta}$ is the accuracy with which a floating female can assess the fitness consequences of the decision, and W_{fB2} and W_{fL} is the expected fitness of a female in a polygynous group and a floating female, respectively. We do this for two reasons: first, it makes biological sense to assume that females are not able to perfectly assess the fitness consequences of their decision. In our model, however, we can investigate the influence of females' decision making accuracy by altering how closely the sigmoidal curve approximates a step-function, i.e. a true binary decision, by changing the value of $\hat{\beta}$. Second, by using a non-binary probability for joining, we can use an adaptive dynamics approach also for the evolution of the mating system (Dieckmann and Law 1996).

Solving the model

We solve the model, given a certain set of globally specified environmental parameters ($\hat{\varepsilon}$, $\hat{\gamma}$, $\hat{\theta}$, etc., see above), by identifying a convergently stable, evolutionary equilibrium, at which the probability of a floating female joining a monogamous pair is optimal (subject to assessment error $\hat{\beta}$ as described above),

and selection gradients on the levels of parental investment by individuals of all classes (C_{mL}, C_{fL}, C_{mB0}, C_{mB1}, C_{fB1}, C_{mB2}, C_{fB2}, respectively) are simultaneously equal to zero.

Unfortunately, we are unable to solve the model analytically. Hence, to identify an equilibrium of the kind described above, we use an iterative solution procedure in which, starting with an arbitrary set of initial levels of parental investment, these values are repeatedly updated by adding to each a multiple of the selection gradient for the trait in question (and replacing the current joining probability with some weighted sum of the existing value and the error-prone optimum at the current demographic equilibrium; cf. Supplements 9 & 11). This procedure is repeated until convergence to an equilibrium, which we take to have been reached when the maximum change in any strategic variable from one iteration to the next falls below some small threshold value (cf. Supplement 20).

Model 2 – allowing for interference among females

Model 2 allows for interference by resident, primary females in the joining decisions of floater females. We do this by considering the fitness consequences of accepting polygyny by floaters (which become joiners (secondary females) upon accepting polygyny with probability $\hat{J}$) for resident females. We thus change the way in which $\hat{J}$ is determined:

Eq. 6: $\hat{J} = \frac{1}{1+e^{-\hat{\beta}\left((1-\hat{\lambda})(W_{fB2}-W_{fL})+\hat{\lambda}(W_{fB2}-W_{fB1})\right)}}$

where $\hat{J}$ is the probability that a floating female joins a monogamous pair, $\hat{\beta}$ is the accuracy with which females can assess the fitness consequences of the decision, $\hat{\lambda}$ is the weight given to the fitness consequences of joining to resident females, and W_{fB2}, W_{fL} , and W_{fB1} is the expected fitness of a female in a polygynous group, a floating female, and a monogamous female, respectively. Thus, high values of $\hat{\lambda}$ shift the values of $\hat{J}$ towards the optimum for monogamous (resident, primary) females, while low values

shift $\hat{f}$ towards the optimum for floaters (joiners or secondary females). Other than substituting Eq. 5 with Eq. 6, Models 1 and 2 are identical (hence, when setting $\hat{\lambda} = 0$, Models 1 and 2 are exactly equivalent).

Model 3 – allowing for fecundity differences between resident females and joiners

Model 3 introduces fecundity asymmetries between resident, primary females and joining, secondary females (which requires tracking eight classes of individual rather than seven; see Supplements 12-19 for details). Specifically, fecundity is calculated differently for residents (Eq. 7a) and joiners (Eq. 7b):

Eq. 7a: $\gamma_{B2r} = \hat{\gamma} * (1 - e^{-(C_{fB2r} + C_{mB2r})})$

Eq. 7b: $\gamma_{B2j} = \hat{\gamma} * \hat{\varphi} * (1 - e^{-(C_{fB2j} + C_{mB2j})})$

where $\hat{\gamma}$ is the global base rate of offspring production, C_{fB2r} is the parental investment of resident (primary) females in polygynous groups, C_{mB2r} is the parental investment of polygynous males in offspring of resident females, $\hat{\varphi}$ is the factor by which fecundity is multiplied for joiner (secondary) females compared to primary females, C_{fB2j} is the parental investment of joiners, and C_{mB2j} is the investment of polygynous males in offspring of joiner females. The lower the value of $\hat{\varphi}$, the more costly it is (in terms of relative fecundity reduction) for a floater female to accept polygyny ($0 \leq \hat{\varphi} \leq 1$).

Model 4 - allowing for mortality differences between resident females and joiners

Model 4 is similar to Model 3, except that there is no fecundity cost of joining (i.e. $\hat{\varphi} = 1$). Instead, secondary, joiner females incur mortality costs compared to primary, resident females. Mortality rates for residents (Eq. 8a) and joiners (Eq. 8b) are given by:

Eq. 8a: $\mu_{fB2r} = \hat{\mu}_{fB} + (C_{fB2r})^2$

Eq. 8b: $\mu_{fB2j} = \hat{\mu}_{fB} * \hat{\tau} + (C_{fB2j})^2$

where $\hat{\mu}_{fB}$ is the baseline mortality of breeding females (see above), C_{fB2r} is the parental investment of resident females in polygynous groups, $\hat{\tau}$ is the factor by which baseline mortality is increased for joiners compared to other breeding females, and C_{fB2j} is the parental investment expended by joiner females. The higher the value of $\hat{\tau}$, the greater the mortality costs of accepting polygyny for floaters compared to other breeding females ($\hat{\tau} \geq 1$).

Comparing the models

In order to compare the predictions of the models with regards to evolving mating decisions and parental investment strategies, we evaluated all four models along the same environmental productivity gradient (i.e. setting $\hat{\gamma}$ to values from 4 to 12 – values lower than 4 always resulted in unviable populations and values larger than 12 did not qualitatively alter the outcomes of the models) with otherwise identical parameter values. Specifically, we used the following conditions for all four models: $\hat{\beta} = 40$, $\hat{\varepsilon} = 20$, $\hat{\theta} = 0.5$, $\hat{\mu}_{mL} = 0.1$, $\hat{\mu}_{fL} = 0.1$, $\hat{\mu}_{mB} = 1$, $\hat{\mu}_{fB} = 1$. We initiated the models with starting values for parental investment of all classes of individuals and joining probability set to 0.5 (in Models 3 and 4, polygynous males have two components to their parental investment (one expended towards offspring of resident females and one expended towards offspring of joiner females) and each was set to 0.25 for a total starting value of 0.5). We found that running the models for 150 iterations proved sufficient for them to converge when using a maximum difference between resident and mutant investments and joining probabilities of 0.1 (i.e. step size (X), see Supplement 20). We thus ran the models for each value of $\hat{\gamma}$ for 150 iterations (number of steps) with a step size (X) of 0.1 (see Supplement 20). For the current

manuscript, we set $\hat{\lambda} = 0.9$ for Model 2. For Model 3, we set $\hat{\varphi} = 0.5$. For Model 4, we set $\hat{\tau} = 2$. We thus compare the predictions of Model 1 (basic) to those of a situation (i) in which fitness consequences of joining decisions to resident females account for 90% of the selective pressure (Model 2 – interference), (ii) in which joiners have half the reproductive potential of other breeding females (Model 3 – reproductive costs), or (iii) in which joiners suffer twice the baseline mortality compared to other breeding females (Model 4 – mortality costs).

Below, we explore how predicted outcomes vary along a gradient of environmental productivity, captured in the model by the baseline level of reproductive output ($\hat{\gamma}$). We focus on this parameter in particular because it exerts a very strong influence on both female mating decisions (and hence on the mating system) and on parental investment. The effects of other ecological parameters, such as female mobility ($\hat{\varepsilon}$), female decision making accuracy ($\hat{\beta}$), and baseline mortalities ($\hat{\mu}_{mL}$, $\hat{\mu}_{fL}$, $\hat{\mu}_{mB}$, $\hat{\mu}_{fB}$), which are much less pronounced, are explored in Supplements 21-25.

Results

The evolution of monogamy

In all four models, adaptive monogamy (indicated by joining probabilities $J < 0.5$, which imply a greater fitness payoff to remaining as a floater than to joining) is found in relatively unproductive environments, i.e. for those values of $\hat{\gamma}$ adjacent to the boundary of population extinction, which results in relatively sparse populations (cf. shaded areas in Figures 2 & 3). However, introducing interference or asymmetries among females extends the range of environments in which monogamy is favoured, with asymmetries having a stronger impact than interference (cf. the greater range of adaptive monogamy for Models 3 and 4, compared to Model 2, compared to Model 1 in Figures 2 & 3).

Sex ratios and mating decisions

As seen in Figure 2B, there are clear shifts in adult sex ratio (ASR; the proportion of all individuals in breeding patches and floater communities that are male) associated with the transition from monogamy to polygyny. However, there is no direct causal relationship between ASR and mating system: in our models, changes in sex ratio and female mating decisions both emerge from the interplay between the underlying demographic factors. Figure 2B reveals that as productivity increases, which intensifies female competition for mating opportunities and thus favours a switch from monogamy to polygyny, the ASR becomes more male biased. This reflects the fact, illustrated in Figure 3, that under polygyny a higher proportion of females than of males are able to become breeders, thereby incurring higher mortality rates than they would do as floaters (we assume $\hat{\mu}_{fL} < \hat{\mu}_{fB}$ and $\hat{\mu}_{mL} < \hat{\mu}_{mB}$, see above). The resulting sex-bias in mean mortality leads to a shift in the overall ratio of males to females. As productivity increases still further, however, the proportion of floaters of both sexes grows, diluting the impact of sex-differences in the number of breeders so that the ASR tends to decline back towards 1:1 (see Figures 2B and 3; see Supplement 25 for an additional discussion of sex ratios in our models).

Mating decisions and total parental investment

The total parental investment predicted by the models typically differs between monogamous pairs and polygynous groups (Figure 4). However, the form of these differences is dependent on the particular model under investigation: in Models 1 and 2, offspring produced in polygynous groups typically receive more parental investment than those produced in monogamous pairs, while the opposite is true for Models 3 and 4 (cf. intercepts in Figure 4). In other words, different routes to monogamy predict different patterns of parental investment in relation to mating status. Crucially, the way in which parental investment changes with transitions to polygyny is also fundamentally different between the different models: as monogamy becomes rarer, parental investment is generally reduced in Models 1 and 2, but increased in Models 3 and 4 (cf. slopes in Figure 4).

What is more, the type of asymmetry between resident (primary) and (secondary) joiner females in polygynous groups determines whether it matters to offspring if their mother is a resident or a joiner (cf. Figure 4B): when joiners suffer from reduced fecundity by comparison with residents, offspring of joiners receive markedly less parental investment than those of residents (due to a complete lack of paternal investment; cf. the discrepancy between the solid and the dashed-and-dotted lines in Figure 4B for Model 3). In contrast, if joiners suffer increased mortality by comparison with residents, offspring produced in polygynous groups receive the same amount of parental investment, irrespective of whether their mother is a resident or a joiner (cf. the perfect overlap of solid and dashed-and-dotted lines in Figure 4B for Model 4).

Mating decisions and sexual conflict over parental investment

Similar to the results for total parental investment (see above), we also record marked differences in the way parental investment is shared among males and females in the different models (Figure 5). However, three general patterns hold for all models: first, parental investment is generally more biased towards females when polygyny is more common across a population (and this pattern holds within both monogamous pairs and polygynous groups). Second, in monogamous pairs, sharing of parental investment is unbiased when monogamy prevails in the population, becomes female-biased as floater densities decrease during the transition towards polygyny, and becomes more egalitarian again, once polygyny is established and floater densities increase (cf. Figure 5A). Third, in polygynous groups, females always expend more parental investment than males, albeit to different degrees depending on the mating system and female densities (cf. Figure 5B).

While the shape of the relationship between female density, mating system switches, and sharing of parental investment in monogamous pairs is similar for all models (cf. Figure 5A), it is overall more female-biased in Models 3 and 4 compared to Models 1 and 2, especially once monogamy ceases to be

adaptive. The same is true in polygynous groups (cf. Figure 5B), with the marked exception of joiner females suffering from reproductive costs of polygyny (Model 3), which are the lone expenders of parental investment, irrespective of the mating system and environmental productivity ($\hat{\gamma}$).

Discussion

We have shown here that applying a demographically explicit, adaptive dynamics approach to the study of female mating decisions and parental investment strategies of both sexes allows for insights that previous work did not provide. Four general conclusions follow from our framework: 1) In the absence of interference among females regarding mating decisions, and where females have identical mortality- and fecundity prospects irrespective of their status as either resident, primary female or secondary, joiner female in a polygynous group, delaying reproduction to achieve monogamous matings is rarely adaptive for females (cf. Model 1 in Figures 2-4). 2) Monogamy is only likely to be favoured in very unproductive environments with low density populations, i.e. close to the edge of population extinction (see Figures 2-4). This is due to reduced competition for solitary males among floating females in low density populations, a finding easily missed when demography is not considered or when analyses focus on sex ratios alone. 3) The range of parameters over which monogamy is favoured can be markedly increased by allowing for either interference by established, resident females with polygynous matings, or by introducing costs of polygyny for joining, secondary females (cf. the different size of shaded areas in Figures 2-4 between Model 1 versus Models 2-4). 4) Different mechanisms by which monogamy is favoured, i.e. either interference by primary females with polygynous matings or reproductive/mortality costs of accepting secondary status, predict different patterns of co-evolution between mating and parental investment decisions (cf. comparisons between Models 2-4 in Figures 4 & 5). Interference among females does little to alter the balance of sexual conflict over male vs female parental investment (cf. Models 1 and 2 in Figures 4 & 5), while asymmetries between primary and secondary females generally

shift the burden of parental investment away from males and more towards females (compare predictions of Models 1 and 2 to those of Models 3 and 4 in Figures 4 & 5). In addition, it matters whether the costs of secondary mating status are assumed to arise from increased mortality or from decreased fecundity. In the former case, males invest equally in all offspring, whereas in the latter case they invest more heavily in offspring of primary mates (compare predictions of Models 3 and 4 in Figures 4B & 5B).

Comparisons with previous theory

The fact that it is difficult in our basic model (Model 1) to find parameter values that favour monogamy is somewhat at odds with the classic work by (Orians 1969) that inspired the setup of our own equations. For Orians, monogamy was generally assumed to be the default best choice for females and he sought to explain how and why polygyny might be favoured. The two major explanations he offered for the existence of polygynous mating were (a) large qualitative differences among males in terms of the resources they could provide to the female (cf. 'environmental quality' and the 'polygyny threshold' in Figure 2 in (Orians 1969)), and (b) an absence of paternal care (which would then favour promiscuity to obtain genetic benefits, as observed in mammals; (Orians 1969) p. 596 prediction 2). In contrast to Orians' assumptions, however, our Model 1 predicts that females should readily accept earlier polygynous breeding rather than delay reproduction to achieve monogamy, and our extensions (Models 2-4) are attempts to explain how and why monogamy might evolve.

While many aspects of our models follow Orians' ideas (e.g. (i) the general benefit of polygyny to males, (ii) the reduced paternal investment ('care' in (Orians 1969)) received by polygynous females, and (iii) fitness consequences of mating decisions to females being the lone determinant of the mating system), there is one marked difference between his work and ours: we set up a demographically explicit model, while Orians only made verbal arguments concerning density dependent effects. This becomes important, because Orians assumed that rejection of a potential mate would not entail large fitness costs

as another mate would readily be available (cf. (Orians 1969) p. 591 condition '(b)'). Our models assume, however, that when one floating focal individual can easily sample additional mating opportunities at little fitness cost (because encounter rate is high and/or floater mortality low), the same will be true of other floater females. This increases density of floating females, with the result that few opportunities for monogamous mating will remain available for the focal individual to take advantage of. In other words, competition among females for monogamous mating opportunities renders polygyny adaptive unless population density is very low, an insight that is easily overlooked outside of demographically explicit modelling approaches (Kokko and López-Sepulcre 2007).

Our analysis is certainly not the first to consider demographic factors in an explicit way. For instance, 'time-in / time-out' models, which usually assume fixed mortality rates for each of the different states an individual can be in (that is either 'in the mating pool' [i.e. ready to mate] or 'out of the mating pool' [i.e. not currently ready to mate, because of parental investment expended in the previous mating, e.g. performing parental care]), allow for a scaling factor to capture the impact of different levels of fecundity and resulting demographic changes (cf. (Clutton-Brock and Parker 1992), (Fromhage and Jennions 2016)). However, such models generally do not consider the effects of interference among females (as opposed to competition that arises indirectly via mate availability), nor do they allow for potential asymmetries among primary and secondary females (populations are assumed to be homogenous and invading mutants to be rare; cf. Methods: Model 1). Consequently, studies of systems that show such features have tended to follow more closely the approach of Orians (1969; see e.g. (Slagsvold and Lifjeld 1994), (Grønstøl et al. 2003)). Our model, we hope, offers a combined approach that allows for interference and asymmetries among females in a demographically explicit framework, in which both OSR and ASR emerge dynamically from the model rather than being specified extrinsically (as for instance in (Grønstøl et al. 2003)).

Implications for empirical work

From an empiricist's point of view, our approach may help guide data collection and experimental design. First, the fact that $\hat{\gamma}$ (environmental productivity) proved to be important in all our models suggests that any investigation of mating systems and parental investment patterns should monitor demographic parameters including population density and female mobility/sociality, as well as the more commonly studied sex ratio ((Kokko and López-Sepulcre 2007); see also (Lukas and Clutton-Brock 2013) for a recent empirical example). While we agree that the ASR is an important ecological factor when investigating mating systems and parental investment (cf. (Kokko and Jennions 2008)), we follow (Fromhage and Jennions 2016) in their conclusion that '[…] explanations for the relationship between the ASR and the proportion of care given by males that invoked a direct causal role for the ASR are misleading' ((Fromhage and Jennions 2016) p. 2). Rather, interactions between parental investment, mating decisions, and sex ratios should be investigated together with demography (broadly interpreted), without *a priori* assumptions about causality. Second, where either costs of polygyny to females or patterns of parental investment cannot easily be measured, our models allow inferences about one from observations of the other. For example, where polygynous males invest in the offspring of resident (primary) and joiner (secondary) females equally, there are unlikely to be fecundity costs to females associated with accepting polygyny (and *vice versa*; cf. Figure 5). Our models may thus help to reveal characteristics of animal breeding systems that are hard to assess directly. Third, because our models allow for the implementation of different functions to describe the relationships between parental investment, reproduction, and mortality, they may serve as analytical tools to unravel these in empirical systems. By running the models with different functions and comparing their outcomes with empirical data, one can identify those functions that best describe the recorded real-world data as likely to be a closer fit to the actual trade-offs that hold in a particular study system.

For example, in pied flycatchers, reproductive costs of polygyny to females, especially to joiners (i.e. *secondary females*), have been reported, but no survival costs were detected (Huk and Winkel 2006). This situation is equivalent to our Model 3. (Huk and Winkel 2006) did not find any evidence of compensation to joiner females from direct (i.e. survival or reproduction) or indirect (i.e. genetic quality indicated by grand offspring performance) fitness consequences. This begs the question why females should ever engage in polygyny in this system. Our models suggest that accepting the costs of polygyny may pay females, if competition for males is high enough and/or environmental conditions are favourable, increasing the relative costs of delaying reproduction (cf. Figures 2 & 3). Testing whether the frequency of polygyny is indeed correlated with population density or average reproductive success either on temporal or geographic scales may thus allow us to explain seemingly maladaptive mating decisions (Hasselquist 1998), (Herényi et al. 2014).

Future modelling possibilities

Our models rely on numerous simplifying assumptions that are at times at odds with real-world observations, and that might be relaxed or modified in future analyses. Four of these simplifications are especially note-worthy: First, we allow only one sex to make decisions about mating, which is likely to be unrealistic (Davies 1989). For example, acorn woodpeckers (Koenig et al. 1984), dunnocks (Davies 1985), lesser spotted woodpeckers (Wiktander et al. 2000), and penduline tits (Persson and Öhrström 1989) have all been reported to simultaneously exhibit various forms of mating within the same population, suggesting that both sexes may often be choosey with regards to mating decisions (Parker 2006). Second, we limit polygyny to a situation where two females are paired with one male, i.e. the OSR can only vary between 1/2 and 1/3 (proportion of males among all breeding individuals). In many polygamous systems, however, much more extreme values of the OSR are observed (e.g. elephant seals (McCann 1980), pipefish (Vincent et al. 1994), primates (Mitani et al. 1996)). Third, other than the differences in territory-

and mate acquisition, we assume males and females to be identical, which is obviously different from real animal systems where (i) females by definition invest into larger gametes (Liker et al. 2015), (ii) the sexes often differ in their physiological ability to invest into offspring (e.g. gestation and lactation in mammals), or (iii) face different limits to their reproductive life span (Heinze 2016). Fourth, we omit certain ecological factors that have been shown to influence parenting and mating decisions, for example spatial or temporal clustering of mates or resources and the costs of territoriality (Ah-King et al. 2005), (Wong et al. 2012). Some of these limitations could potentially be addressed by either using different reproduction- or mortality functions (e.g. introducing different scaling factors of parental investment for males and females) or by extending the models (e.g. allowing more females to settle per territory or introducing a temporal structure). However, such work is outside of the scope of the current manuscript.

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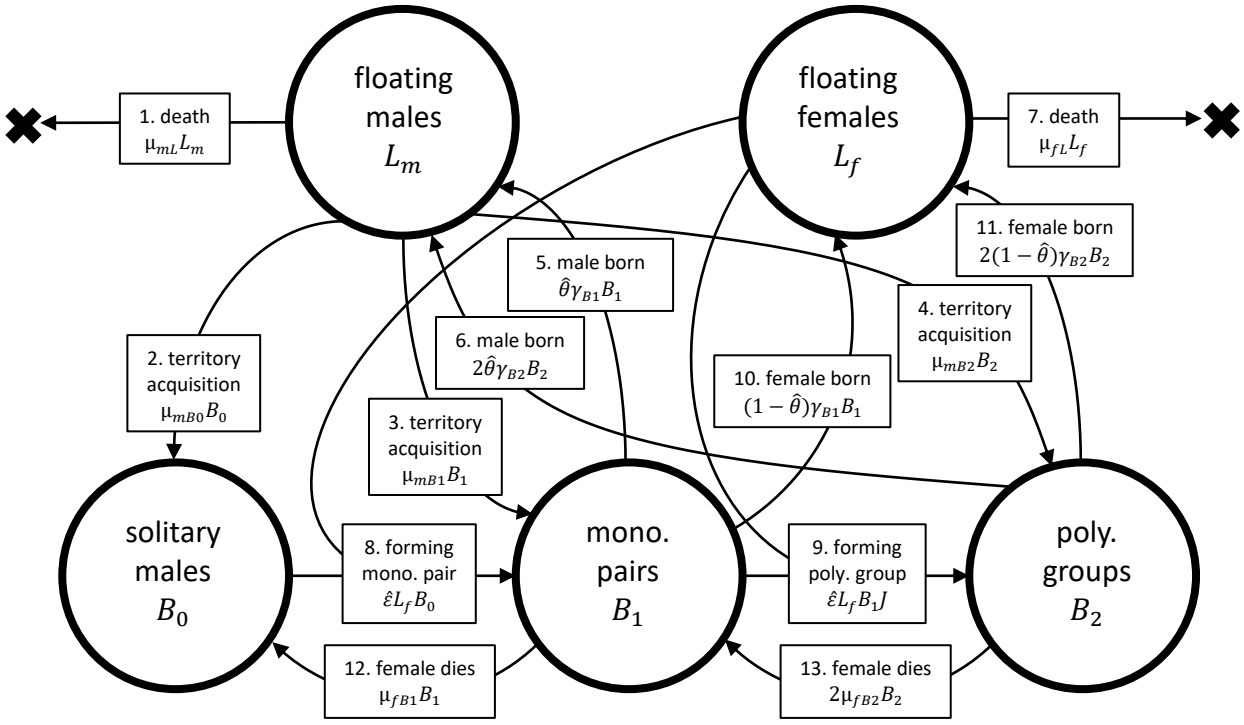

Figure 1: Schematic overview of the model, highlighting the ways in which frequencies of territory types and densities of floaters (and consequently numbers of males and females) change. Throughout the text, densities of male and female floaters are denoted as L_m and L_f, respectively. The frequencies of breeding territories with a solitary male (no female), a monogamous pair, and a polygynous group are denoted in the text as B_0, B_1, and B_2, respectively. Densities of floating males decrease when floaters die (1; at rate $\mu_{mL}L_m$), when solitary males die and floaters acquire their territory (2; at rate $\mu_{mB0}B_0$), when monogamous males die and floaters acquire their territory (3; at rate $\mu_{mB1}B_1$), or when polygynous males die and floaters acquire their territory (4; at rate $\mu_{mB2}B_2$). Densities of floating males increase when surviving male offspring are produced by a female in a monogamous pair (5; at rate $\hat{\theta}\gamma_{B1}B_1$), or by a female in a polygynous group (6; at rate $2\hat{\theta}\gamma_{B2}B_2$). Densities of floating females decrease when floaters die (7; at rate $\mu_{fL}L_f$), when floating females encounter a solitary male and join it to form a monogamous pair (8; at rate $\hat{\varepsilon}L_fB_0$), and when floating females encounter a monogamous pair and decide to join it to form a polygynous group (9; at rate $\hat{\varepsilon}L_fB_1J$). Densities of floating females increase when surviving female

offspring are produced by a female in a monogamous pair (10; at rate $(1-\hat{\theta})\gamma_{B1}B_1$), or by a female in a polygynous group (11; at rate $2(1-\hat{\theta})\gamma_{B2}B_2$). The frequency of territories with a solitary male decreases when floating females encounter solitary males and join them to form a monogamous pair (8; at rate $\hat{\varepsilon}L_f B_0$). The frequency of territories with a solitary male increases when females in monogamous pairs die (12; at rate $\mu_{fB1}B_1$). The frequency of territories with monogamous pairs decreases when females in monogamous pairs die (12; at rate $\mu_{fB1}B_1$), and when floating females encounter monogamous pairs and join them to form a polygynous group (9; at rate $\hat{\varepsilon}L_f B_1 J$). The frequency of territories with a monogamous pair increases when floating females encounter solitary males and join them to form a monogamous pair (8; at rate $\hat{\varepsilon}L_f B_0$), and when females in polygynous groups die (13; at rate $2\mu_{fB2}B_2$). The frequency of territories with a polygynous group decreases when females in polygynous groups die (13; at rate $2\mu_{fB2}B_2$). The frequency of territories with polygynous groups increases when floating females encounter monogamous pairs and decide to join them to form a polygynous group (9; at rate $\hat{\varepsilon}L_f B_1 J$).

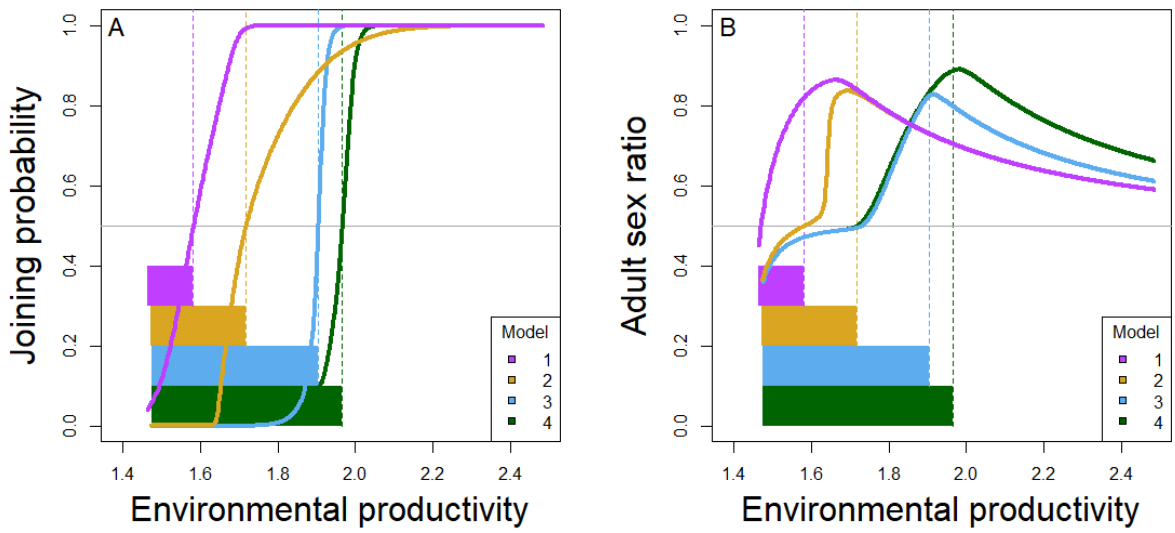

Figure 2: The influence of environmental productivity (x-axis in both panels: $\log \hat{\gamma}$) on (A) female mating decisions and (B) the adult sex ratio (ASR; proportion of males) for all four models. In (A) solid lines represent selected joining probabilities of floating females, in (B) solid lines represent the ASR. Horizontal thin grey lines indicate joining indifference (A; $J = 0.5$) and an even ASR (B; 50% males). Vertical dashed lines indicate the value of $\hat{\gamma}$ at which monogamy ceases to be adaptive for females, and shaded areas represent the range of values of $\hat{\gamma}$ for which $J < 0.5$ (i.e. adaptive monogamy) is observed.

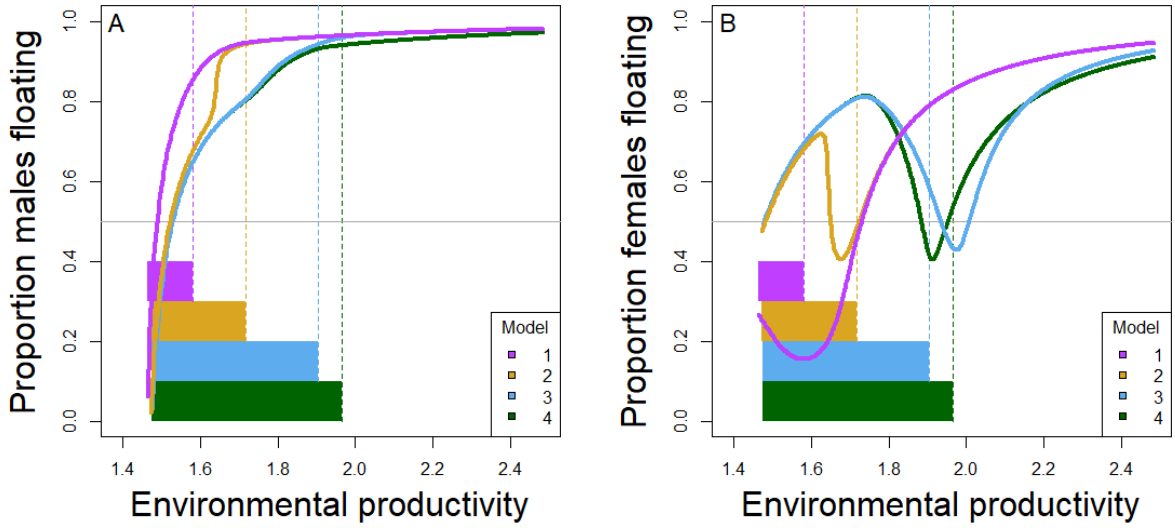

Figure 3: The proportion of adults floating for males (A) and females (B) along the environmental productivity gradient (x-axis in both panels: $\log \hat{\gamma}$) for all four models. Values close to 0 indicate that most individuals are breeding, a value of 0.5 indicates that there is one floater per breeder (thin grey lines), and a value close to 1 indicates that most individuals float. Solid lines represent the proportion of floaters, dashed lines indicate the value of $\hat{\gamma}$ at which monogamy ceases to be adaptive for females, and shaded areas represent the range of values of $\hat{\gamma}$ for which $J < 0.5$ (i.e. adaptive monogamy) is observed.

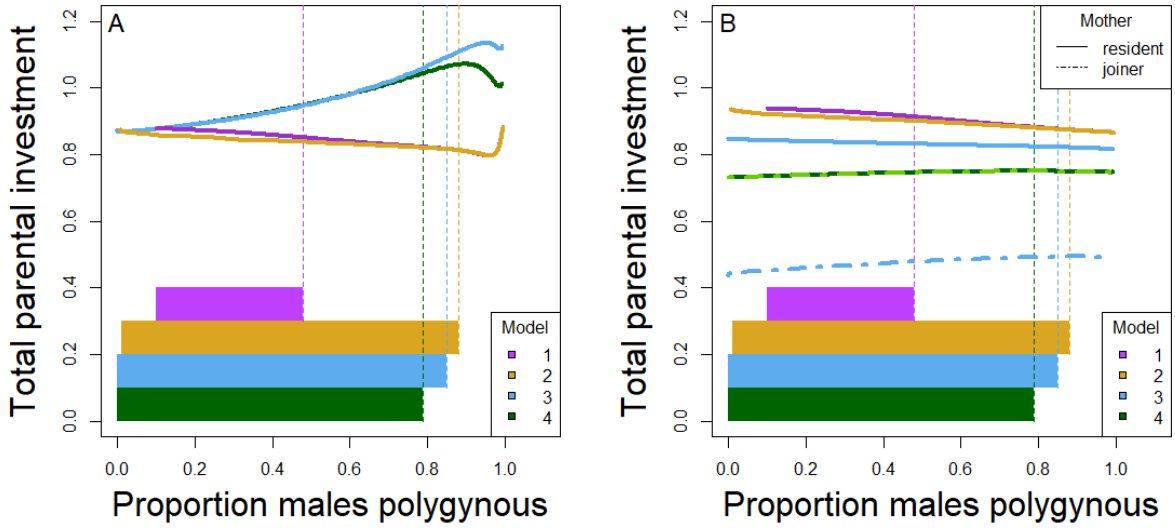

Figure 4: The total parental investment in (A) monogamous pairs and (B) polygynous groups as a function of the mating system for all four models. The mating system is characterised as the proportion of breeding males that are mated polygynously (x-axis). Thus, an x-value of 0 represents a purely monogamous population, while a value of 1 indicates a purely polygynous one. In both graphs, vertical dashed lines indicate the proportion of polygynously mated males at the point at which monogamy ceases to be adaptive for females, and shaded areas represent the range of proportions of polygynously mated males for which $J < 0.5$ (i.e. adaptive monogamy) is observed. In (A) solid lines represent total parental investment (paternal investment + maternal investment). In (B) solid lines represent total parental investment received by offspring of resident females, and dashed-and-dotted lines represent total parental investment received by offspring of joiner females.

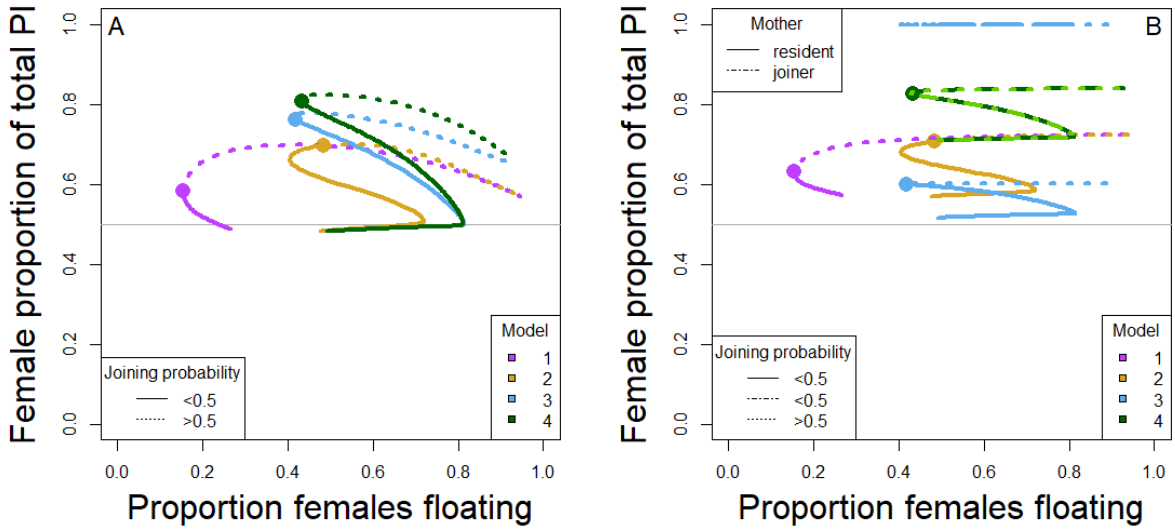

Figure 5: The proportion of total parental investment (PI) expended by females in (A) monogamous pairs and in (B) polygynous groups as a function of female density (x-axis; floating females per breeding female). Thus, an x-value near 0 represents low density and most adult females breeding, a value near 1 represents high density and the majority of adult females floating. Similarly, a y-value of 1 indicates the female being the lone expender of PI, a value of 0.5 indicates perfectly egalitarian sharing among males and females (grey lines), and a value of 0 indicates the male being the lone expender of PI. In both graphs, large circles represent those points at which monogamy ceases to be adaptive for females. Consequently, solid and dashed-and-dotted lines represent areas in which monogamy is adaptive ($J < 0.5$), while dotted lines represent areas in which polygyny is adaptive ($J > 0.5$). In (A) solid and dotted lines represent a breeding female's share of total PI. In (B) solid lines represent the share of total PI for resident females, and dashed-and-dotted lines represent the share of total PI for joiner females (dotted lines give the respective values for $J > 0.5$, cf. above).